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The tadpoles of the brown frogs *Rana [graeca] graeca* and *Rana [graeca] italica* (Amphibia, Anura)

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External morphology and buccopharyngeal characters of the tadpoles of *Rana [graeca] graeca* and *Rana [graeca] italica* are described in detail. Both characterize the larvae as well adapted to flowing waters. The most distinctive oral and buccal features are the increased number of tooth rows, the high number of papillae in both buccal floor and buccal roof arena, and the large prelingual palps with elongate lobes.

Larvae from Italy resemble those from Greece. However, samples from both countries differ slightly but significantly in a variety of features. This supports the existence of two taxons, subspecies or species, *graeca* for the populations of the Balkans and *italica* for those of the Apennines.

INTRODUCTION

Rana graeca Boulenger, 1891 (Greek frog, stream frog) is the only European anuran which was first recognized by its larva. The story of the tadpoles' discovery by the French batrachologist Louis-François HÉRON-ROYER is reported by BOULENGER (1891a) and confirmed by a letter from HÉRON-ROYER to Raymond ROLLINAT, dated 27 September 1891 (library, Laboratoire des Reptiles et Amphibiens, Muséum national d'Histoire naturelle, Paris), where he writes: "Je viens de recevoir une lettre de Boulenger qui m'annonce une nouvelle grenouille pour la faune Européenne, sur un têtard de Grèce que je lui ai déterminé n'étant ni *R. fusca* ni *R. Latastei.* Il vient d'en faire une *Rana graëca.*"

Geographical disjunction (map in ARNOLD & BURTON, 1978) and morphometric divergences between adult specimens from the Balkans and from the Apennines gave rise to discussions on intraspecific variation (ARNOLD & BURTON, 1978) and taxonomic status (LANZA, 1983). The establishment by DUBOIS (1987)[1] of two subspecies, *R. graeca graeca* (Balkans) and *R. graeca italica* (Apennines), was based on external morphometric differences in adults, whereas the suggested raising of *italica* to specific rank (PICARIELLO et al., 1990; CAPULA, 1991) resulted from allozyme studies.

Literature on larval morphology of *R. graeca* is scarce. Oral disks are depicted in BOULENGER (1891b) and GÜNTHER (1985), well developed larvae in BOULENGER (1891b) and BESKOV (1970). The former additionally provided a short description and differential diagnosis and the latter contributed to the knowledge of the tadpole's biology. Both authors refer to a small number of Balkan specimens only. No further morphological investigations are available and there are no comparative data on tadpoles from Italy.

The primary goal of the present paper is to describe the external and buccopharyngeal characters of *graeca* and *italica* larvae in the process of development. This is done for a variety of features (also for those where no significant differences between tadpoles from the Balkans and the Apennines were found), to make data available for comparison with other South European brown frog species.

MATERIAL AND METHODS

Specimens from five Greek and seven Italian localities were investigated (Table I). Number of specimens is 212 for detailed morphometric analysis, 364 for size-stage diagram (fig. 4), and 282 for tooth rows counts. Description of buccopharyngeal structures refers to five tadpoles each (stages 36-38) from both Italy and Greece (asterisks in Table I) and is based on stereomicroscopy (n = 6) and scanning electron microscopy (n = 4).

External morphology is described using established parameters introduced by BOULENGER (1897-1898), and defined in more detail by GRILLITSCH (1984) and GRILLITSCH et al. (1989). The measurements do not represent true distances but projections to the tadpole's frontal and sagittal planes respectively (Table II). Distances between pupillae or nostrils mean distances between the centres of these organs. Tooth rows of both upper and lower lip are numbered from the margin towards the centre of the oral disk, as is done in the classic terminology of BOULENGER (1891b). The length of a tooth row is defined as the straight distance between its ends in the expanded oral disk. For tooth rows formula (number of upper rows / number of lower rows), rows are counted as one whether continuous or interrupted, uni- or bilateral.

1. Several authors (PICARIELLO et al., 1990; CAPULA, 1991; DUELLMAN, 1993) credit the name *italica* to "DUBOIS (1985)", although the paper where this name first appeared was published on 26 January 1987 (DUBOIS, 1988a), and should therefore be quoted as "DUBOIS (1987)".

Table I. — Material investigated. MNHN: Muséum national d'Histoire naturelle, Paris; NMW: Naturhistorisches Museum Wien; *: samples used for buccopharyngeal analysis; habitat: B, brook; T, torrent; R, river; P, pond; morphometry: specimens used for detailed morphometric analysis (Table III); size-stage graph: specimens used in size-stage graph (fig. 4); tooth rows counts: specimens used in tooth rows counts; n: number of specimens; RS: range of GOSNER's (1960) stages of specimens.

Specimens series	Country and region	Locality	Habitat	Date	Morphometry n (RS)	Size-stage graph n (RS)	Tooth rows counts n (RS)
MNHN 1985.1777-1815	Greece, Peloponnissos, Ahaia	Kato Vlassia (760-770 m)	T	13.08.82	34 (28-39)	36 (28-40)	34 (28-40)
NMW 29181:1-20	Greece, Peloponnissos, Ahaia	Krathis potamos near Zivlos (550 m)	B	06-10.08.84	12 (31-39)	15 (31-43)	14 (31-41)
MNHN 1985.1817-2024 *	Greece, Peloponnissos, Arkadia	Kalomeri (980 m)	T	14.08.82	66 (29-39)	182 (29-45)	117 (29-41)
NMW 27637:1-20	Greece, Peloponnissos, Ilia	Oros Minthi near Nea Figalia (750 m)	B	16.08.83	15 (27-39)	26 (27-41)	24 (27-41)
NMW 29180:1-20	Greece, Peloponnissos, Korinthia	Olvios potamos near Feneos (800 m)	B	06-10.08.84	10 (28-39)	10 (28-41)	10 (28-41)
MNHN 1985.1756-1775	Italy, Abruzzo, Teramo	Fiume Salinello (1040 m)	T	08.08.85	3 (34-39)	20 (34-44)	12 (34-41)
MNHN 1985.1719	Italy, Basilicata, Potenza	Fontana d'Eboli (1010 m)	B	02.08.82	1 (30)	1 (30)	1 (30)
MNHN 1985.1720	Italy, Basilicata, Potenza	Pecorone (800 m)	T	02.08.82	1 (37)	1 (37)	1 (37)
MNHN 1985.1504-1560 *	Italy, Calabria, Cosenza	Cosentino (1140 m)	T	22-23.07.82	57 (28-39)	57 (28-39)	55 (28-39)
MNHN 1985.1564-1674	Italy, Calabria, Cosenza	Fiume Savuto (1070 m)	R + P	24.07.82	1 (37)	1 (37)	-
MNHN 1985.1678-1691	Italy, Lazio, Frosinone	Vallegrande (530-570 m)	T	01.08.82	12 (37-39)	14 (37-40)	14 (37-40)
MNHN 1985.1776	Italy, Marche, Ascoli Piceno	Trisungo (630 m)	B	09.08.85	-	1 (42)	-

Table II. – Definition of distances measured, including explanation of abbreviations used. P: projection to frontal (F) or sagittal (S) plane.

Abbreviation	Definition	P
HT	Maximum height of tail (including upper and lower tail fin)	S
IMP	Number of inframarginal oral papillae	
LF	Maximum height of lower (ventral) tail fin	S
LTR1	Length of first (outermost) tooth row of lower lip	
LTR2	Length of second tooth row of lower lip	
MP	Number of marginal oral papillae	
NN	Internarial distance	F
NP	Naro-pupillar distance	F
OD	Maximum width of oral disk	F
PP	Interpupillar distance	F
RN	Rostro-narial distance	F
SS	Distance: tip of snout - opening of spiracle	S
SU	Distance: tip of snout - insertion of dorsal tail fin	S
SV	Distance: tip of snout - vent (snout-vent length)	S
TL	Distance: tip of snout - tip of tail (total length)	S
UF	Maximum height of upper (dorsal) tail fin	S
UTR1	Length of first (outermost) tooth row of upper lip	
UTR2I	Length of median gap between portions of second tooth row of upper lip	F
UTR2P	Length of one portion of second tooth row of upper lip	F
VS	Distance: vent - opening of spiracle	S
VT	Distance: vent - tip of tail (length of tail)	S

Nomenclature of buccopharyngeal structures is largely in accordance with Wassersug (1976, 1980); definition of developmental stages follows Gosner (1960).

Tadpoles examined comprise developmental stages 27 through 45; detailed morphometric analysis was restricted to stages 28-39. Since body proportions change during growth, morphometric data have to be accompanied by the size or developmental stage they refer to. In the present paper the assignment to size classes was preferred because of statistical reasons. Since there is a fair positive linear correlation between size and developmental stages 27 through 39 (fig. 4), they are easily convertible.

Measurements were done optically with a digital display length-measuring unit (Wild MMS 235). Preparation for SEM examination (Jeol JSM-35 CF) comprised dehydration (ethanol), critical-point-drying (acetone, liquid carbondioxide), and gold sputter surface-coating.

Statistical analyses were processed using SPSS-X and SAS. Significances (α) were calculated by means of Student t test and Mann-Whitney U test. Selection rule for discriminant analysis (fig. 10) with stepwise variable selection was: maximize minimum Mahalanobis distance. For both the pooled Greek and the pooled Italian samples, homogeneity was proved by Kruskal-Wallis ANOVA for each measurement within each of the six size classes, where sufficient material was available. For references concerning Haldane's coefficient of variation (Table III), see DELAUGERRE & DUBOIS (1985).

RESULTS

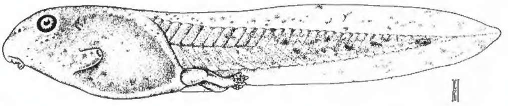
GENERAL APPEARANCE, COLOUR AND PATTERN (PRESERVED SPECIMENS) (FIGS. 1-3)

In Greek and Italian tadpoles, the slightly depressed ovoid body continuously extends into the robust, fairly elongate tail which lacks a marked constriction at its base. Both dorsal and ventral caudal fins are low and slightly convex with almost parallel edges. The height of the trunk is not or not clearly exceeded by that of the tail fin which is more or less tapering but never acutely pointed and sometimes even obtuse. As is typical of tadpoles of the subgenus *Rana*, the spiracular tube is sinistral and directed backwards and slightly upwards. It opens about halfway between tip of snout and vent, more frequently a little closer to the anterior than to the posterior end of the trunk, especially in advanced developmental stages. The vent opens subdextral, close to the edge of the ventral fin. The eyes are moderately sized, close to one another, not visible from below.

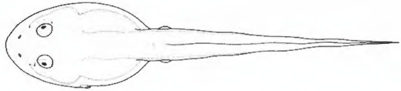
The trunk is dark greyish-brown above due to a close speckling with black. The ventral parts and the muscular portion of the tail are much lighter, the latter speckled with black. Caudal fins are greyish, transparent, with small dark spots or arborescent markings, mainly in the dorsal portion. There are neither distinct changes in colour or pattern during larval development, nor are there differences between Greek and Italian specimens.

SIZE AND PROPORTIONS OF TRUNK AND TAIL (TABLE III)

The tadpoles on which this study is based were all collected in the months of July and August (Table I), i.e. several months after the breeding period, which occurs in February to April in Italy (BAGNOLI, 1985; PICARIELLO et al., 1993) as well as in the Balkans (BESKOV, 1970; NÖLLERT & NÖLLERT, 1992). Total lengths (TL) of the smallest tadpoles examined were 20.2 mm (Italy, stage 28) and 21.5 mm (Greece, stage 28). So we cannot contribute to the size of hatchlings which is 9.1-9.5 mm for Bulgarian specimens (BESKOV, 1970). Maximum TL were 48.5 mm (Italy, stage 41) and 58.2 mm (Greece, stage 41), exceeding the maxima compiled from literature (45 mm, GÜNTHER, 1985; 46.3 mm,



1



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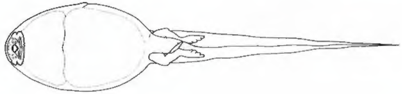

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Figs. 1-3. — Stage 38 *graeca* tadpole from Krathis potamos, Greece (NMW 29181): (1) lateral view; (2) dorsal view; (3) ventral view.

Beskov, 1970; 48 mm, Boulenger, 1891a-b; 50 mm, Bagnoli, 1985). As in adults, the average TL of Greek larvae clearly surpasses that of Italian ones (fig. 4), what is significant ($\alpha \leq 0.05$) in stages 29, 31, 35, 36, 39, 40, 41.

Mean values of VT/SV varied with TL increasing from 0.78 to 1.53 in Italian, and from 0.92 to 1.45 in Greek larvae, exceeding 0.6 calculated from Boulenger's (1891a) table. In size classes TL 30.0-49.99 mm, Italian tadpoles have longer tails than Greek ones ($\alpha \leq 0.05$).

The dorsal tail fin barely reaches the trunk. In Italian tadpoles, the dorsal fin generally extends a little more towards the trunk, whereas in Greek specimens it is restricted to the tail region. This difference in ratio SV/SU is significant ($\alpha \leq 0.01$) in size classes TL 35.0-44.99 mm.

Older (longer) larvae have relatively lower tail fins. The means of VT/HT vary from 1.46 (young larvae) to 2.88 (advanced stages) in Italian tadpoles, and from 2.26 to 3.81 in Greek specimens, respectively, indicating conspicuously higher fins in Italian larvae. These differences are significant ($\alpha \leq 0.05$) in specimens longer than TL 25.0 mm.

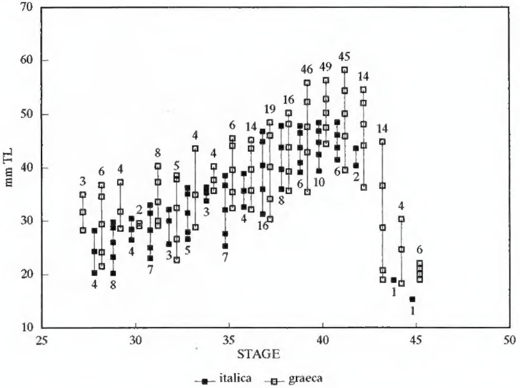

Fig. 4. — Size-stage graph, showing correlation of size (TL) and developmental stage in *italica* and *graeca* tadpoles, including mean value, range, standard deviation and sample size.

On the average, in Italian individuals the heights of dorsal and ventral tail fins are almost the same (UF/LF around 1.0). In Greek tadpoles, the dorsal fin is usually higher than the ventral one (means of UF/LF 1.11-1.34). Differences are significant ($\alpha \leq 0.01$) in animals longer than TL 30 mm.

Ratios HT/UF and SS/VS reveal no significant differences between Italian and Greek tadpoles.

POSITION OF EYES AND NARES, WIDTH OF ORAL DISK

The nares are positioned closer to the tip of the snout than to the eyes. Mean values of RN/NP are a little higher in Greek than in Italian larvae, meaning the nares of the Italian being closer to the tip of the snout ($\alpha \leq 0.1$ in size classes TL 30.0-34.99 mm and TL 40.0-49.99 mm). Ratio PP/NN is not significantly different between Italian and Greek larvae.

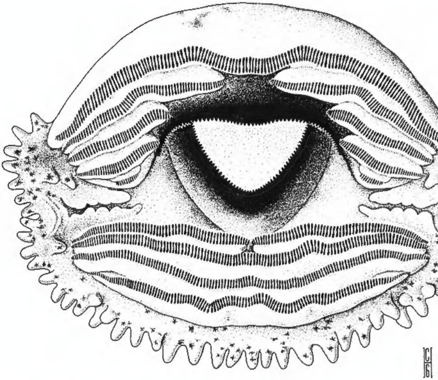

Fig. 5. — Oral disk of a *graeca* tadpole (stage 38) from Krathis potamos, Greece (NMW 29181), stage 38.

BOULENGER (1891a-b) mentions that *R. graeca* tadpoles differ from their European "congeners in having the mouth quite as wide as the interorbital space". Mean values of PP/OD vary from 1.05 to 1.18. Greek tadpoles show a comparatively wider oral disk ($\alpha \leq 0.05$) in size classes TL > 40 mm.

ORAL DISK (FIGS. 1, 3, 5, 6)

The *oral disk* is in ventral subterminal position. It is expanded laterally and of ovoid or rectangular shape. Marginal peribuccal papillae (MP) are restricted to the lateral corners and the posterior margin of the oral disk, and are basically arranged in a single row at a density of 9-10 per millimetre on the posterior margin. In the lateral corners, besides solitary inframarginal papillae (IMP), two papillate ridges are descending towards the beak on each side (figs. 5, 6).

Table III. — Descriptive statistics of selected parameters describing *graeca* (G) and *italica* (I) larvae. Size classes are according to the value of TL (mm). n: number of specimens; min: minimum value; med: median value; $\bar{x}$: mean value; max: maximum value; Sx: standard error of the mean, Sd: standard deviation; V_H: HALDANE's coefficient of variation. For further abbreviations see Table II.

Size class	20.0-24.99		25.0-29.99		30.0-34.99		35.0-39.99		40.0-44.99		45.0-49.99		50-54.9	55-55.9
Samples	I	G	I	G	I	G	I	G	I	G	I	G	G	G
Stage														
n	6	2	19	12	15	16	14	34	12	23	8	38	11	2
min	28	28	28	27	30	27	33	27	37	31	37	35	38	37
med	29	30	30	29/30	34	35/36	36/37	36	37	37	38	39	39	38
max	31	32	35	33	37	37	39	39	39	39	39	39	39	39
TL														
n	6	2	19	12	15	16	14	34	12	23	8	38	11	2
min	20.20	21.50	25.10	26.10	30.30	30.00	35.10	35.00	40.80	40.20	45.20	45.10	50.20	55.40
$\bar{x}$	22.43	22.10	27.34	28.58	32.56	32.31	37.25	37.25	42.91	42.81	46.78	48.07	51.56	55.60
max	24.20	22.70	29.80	29.60	34.50	34.50	39.10	39.80	44.50	44.90	47.90	49.90	54.60	55.80
Sx	0.73		0.34	0.28	0.31	0.38	0.39	0.26	0.39	0.32	0.36	0.22	0.42	
Sd	1.78		1.49	0.96	1.21	1.50	1.45	1.50	1.33	1.53	1.01	1.36	1.39	
V_H	8.3		5.5	3.5	3.8	4.7	4.0	4.1	3.2	3.6	2.2	2.9	2.8	
SV														
n	6	2	19	12	15	16	14	34	12	23	8	38	11	2
min	11.40	10.70	11.40	12.00	13.70	13.40	14.70	15.30	16.60	17.40	17.00	18.30	20.20	22.40
$\bar{x}$	12.73	11.60	13.34	14.23	15.00	15.76	16.22	16.92	18.10	19.24	18.49	20.20	21.26	22.75
max	14.80	12.50	15.20	19.40	16.00	18.90	17.80	19.60	19.30	20.60	19.40	22.40	23.30	23.10
Sx	0.56		0.24	0.51	0.17	0.33	0.24	0.18	0.25	0.20	0.34	0.19	0.27	
Sd	1.38		1.04	1.78	0.67	1.30	0.90	1.06	0.87	0.95	0.95	1.17	0.91	
V_H	11.3		7.9	12.8	4.5	8.4	5.7	6.3	4.9	5.0	5.3	5.8	4.4	
VT/SV														
n	6	2	19	12	15	16	14	34	12	23	8	38	11	2
min	0.51	0.82	0.69	0.48	0.97	0.41	1.16	0.88	1.15	1.09	1.43	1.09	1.22	1.40
$\bar{x}$	0.78	0.92	1.06	1.03	1.17	1.00	1.30	1.21	1.38	1.23	1.53	1.39	1.43	1.45
max	1.10	1.01	1.42	1.36	1.41	1.38	1.51	1.44	1.68	1.43	1.71	1.64	1.58	1.49
Sx	0.09		0.05	0.06	0.03	0.07	0.03	0.02	0.04	0.02	0.04	0.02	0.03	
Sd	0.21		0.20	0.21	0.11	0.27	0.12	0.11	0.14	0.11	0.11	0.15	0.10	
V_H	25.40		18.20	19.80	9.60	26.40	9.40	9.20	10.40	9.00	6.70	10.90	6.40	
SV/SU														
n	6	2	18	11	14	16	14	34	12	23	8	33	10	2
min	1.13	0.99	1.05	1.01	0.85	0.99	0.98	0.97	1.08	1.05	1.06	0.91	1.04	1.06
$\bar{x}$	1.25	1.06	1.24	1.18	1.23	1.18	1.21	1.12	1.26	1.16	1.16	1.16	1.12	1.21
max	1.50	1.13	1.51	1.34	1.38	1.54	1.44	1.28	1.45	1.28	1.35	1.45	1.24	1.35
Sx	0.05		0.03	0.04	0.04	0.03	0.03	0.01	0.03	0.01	0.04	0.02	0.02	
Sd	0.13		0.14	0.12	0.14	0.14	0.13	0.07	0.11	0.07	0.10	0.10	0.06	
V_H	10.00		10.60	9.50	10.80	11.20	10.10	6.30	8.10	5.20	8.00	7.80	4.60	

SS/VS														
n	6	2	18	11	14	16	14	34	12	23	8	33	10	2
min	0.79	0.99	0.80	0.80	0.77	0.79	0.79	0.72	0.75	0.73	0.75	0.70	0.63	0.76
x	0.96	1.00	0.93	0.95	0.92	0.90	0.91	0.90	0.92	0.86	0.91	0.91	0.89	0.82
max	1.05	1.01	1.28	1.34	1.05	1.00	1.12	1.24	1.01	1.05	1.08	1.17	1.04	0.88
Sx	0.05		0.03	0.04	0.02	0.02	0.03	0.02	0.02	0.02	0.04	0.02	0.04	
Sd	0.11		0.10	0.14	0.08	0.06	0.10	0.11	0.08	0.09	0.12	0.09	0.12	
V_H	10.90		10.90	14.00	8.90	6.80	11.20	12.30	8.90	10.60	13.60	10.00	12.70	
VT/HT														
n	6	2	18	11	14	16	14	34	12	23	8	33	10	2
min	0.97	1.78	1.30	1.28	1.66	1.00	2.10	1.88	2.27	2.88	2.25	2.90	3.51	2.97
$\bar{x}$	1.46	2.26	2.09	2.44	2.24	2.47	2.52	3.22	2.55	3.35	2.88	3.54	3.81	3.31
max	1.89	2.73	2.83	3.31	2.78	3.58	3.39	3.91	2.99	3.92	3.19	4.23	4.26	3.64
Sx	0.15		0.11	0.15	0.07	0.17	0.10	0.08	0.07	0.07	0.11	0.06	0.08	
Sd	0.36		0.47	0.49	0.25	0.69	0.36	0.48	0.23	0.34	0.30	0.34	0.26	
V_H	23.50		21.80	19.40	10.10	27.10	14.10	14.70	8.80	10.00	10.00	9.40	6.70	
HT/UF														
n	6	2	17	11	14	16	13	34	12	23	8	33	10	2
min	3.03	3.09	2.90	2.98	2.91	2.66	2.76	2.74	2.69	2.99	2.84	2.95	2.92	3.61
$\bar{x}$	3.32	3.51	3.47	3.49	3.34	3.27	3.31	3.47	3.38	3.58	3.20	3.55	3.62	3.62
max	3.92	3.92	4.72	3.96	3.74	4.53	3.74	4.79	4.09	4.64	3.71	4.80	4.88	3.62
Sx	0.13		0.12	0.10	0.07	0.11	0.08	0.08	0.12	0.08	0.11	0.07	0.20	
Sd	0.31		0.51	0.32	0.26	0.46	0.30	0.47	0.41	0.40	0.31	0.39	0.64	
V_H	8.80		14.60	8.80	7.60	13.70	8.90	13.40	12.10	11.00	9.30	10.80	17.30	
UF/LF														
n	6	2	17	11	14	16	13	33	12	23	8	32	10	2
min	0.79	1.16	0.62	0.82	0.83	0.78	0.90	0.83	0.82	0.88	0.01	0.01	0.90	1.09
x	0.98	1.34	0.97	1.11	1.00	1.25	1.10	1.26	1.03	1.24	0.99	1.26	1.34	1.10
max	1.10	1.52	1.34	1.32	1.23	1.63	1.58	1.73	1.26	1.60	1.23	1.73	1.83	1.11
Sx	0.05		0.04	0.05	0.03	0.06	0.06	0.04	0.04	0.04	0.14	0.05	0.08	
Sd	0.11		0.18	0.17	0.12	0.23	0.20	0.21	0.13	0.20	0.40	0.31	0.26	
V_H	10.60		19.00	14.90	11.20	18.70	21.10	16.80	11.90	15.50	7.40	15.60	18.40	
PP/NN														
n	6	2	18	11	14	14	14	33	12	23	8	33	10	2
min	1.43	1.49	1.22	1.29	1.33	1.33	1.34	1.35	1.46	1.47	1.52	1.46	1.61	1.66
$\bar{x}$	1.50	1.50	1.41	1.45	1.50	1.53	1.64	1.58	1.60	1.58	1.66	1.67	1.74	1.67
max	1.69	1.51	1.68	1.55	1.69	1.74	2.12	2.10	1.79	1.72	1.81	1.95	1.85	1.68
Sx	0.04		0.02	0.03	0.03	0.02	0.07	0.03	0.03	0.01	0.04	0.02	0.02	
Sd	0.10		0.10	0.08	0.11	0.11	0.28	0.19	0.10	0.07	0.11	0.13	0.08	
V_H	6.30		6.50	5.70	6.80	7.30	16.80	12.10	5.80	3.80	6.20	7.20	4.10	
RN/NP														
n	6	2	18	11	14	16	14	34	12	23	8	33	10	2
min	0.49	0.64	0.45	0.48	0.50	0.56	0.47	0.46	0.37	0.45	0.46	0.47	0.42	0.58
x	0.66	0.65	0.59	0.63	0.61	0.69	0.67	0.68	0.57	0.65	0.55	0.63	0.61	0.59
max	0.88	0.65	0.75	0.86	0.81	0.87	0.94	0.85	0.72	0.81	0.70	0.93	0.68	0.60
Sx	0.06		0.02	0.03	0.02	0.02	0.04	0.02	0.03	0.02	0.03	0.02	0.03	
Sd	0.14		0.08	0.11	0.09	0.10	0.14	0.09	0.11	0.10	0.08	0.10	0.08	
V_H	20.50		12.00	16.20	13.30	13.20	19.80	13.30	17.90	15.60	13.10	14.40	13.40	

PP/OD														
n	6	2	17	11	14	16	14	33	12	23	8	33	10	1
min	1.01	1.05	0.95	0.86	0.91	0.85	0.95	0.88	1.12	0.90	1.21	0.98	1.01	1.16
$\bar{x}$	1.12	1.14	1.08	1.05	1.13	1.14	1.15	1.18	1.26	1.18	1.34	1.11	1.15	
max	1.24	1.23	1.20	1.21	1.30	1.40	1.32	1.36	1.45	1.40	1.45	1.26	1.26	1.16
Sx	0.04		0.02	0.03	0.03	0.04	0.03	0.02	0.03	0.03	0.03	0.02	0.02	
Sd	0.10		0.08	0.11	0.11	0.14	0.12	0.12	0.10	0.15	0.10	0.08	0.07	
V_H	8.40		6.60	10.70	9.90	11.60	9.70	10.30	8.10	12.00	6.90	7.30	6.20	
NN/OD														
n	6	2	17	11	14	14	14	34	12	23	8	33	10	1
min	0.68	0.70	0.68	0.62	0.63	0.61	0.46	0.51	0.72	0.56	0.71	0.54	0.60	0.69
$\bar{x}$	0.75	0.76	0.78	0.73	0.76	0.75	0.72	0.76	0.79	0.75	0.81	0.67	0.66	
max	0.83	0.82	0.89	0.82	0.87	0.87	0.84	0.92	0.84	0.90	0.89	0.80	0.73	0.69
Sx	0.02		0.01	0.02	0.02	0.02	0.03	0.02	0.01	0.02	0.02	0.01	0.01	
Sd	0.06		0.05	0.07	0.08	0.08	0.12	0.10	0.04	0.10	0.06	0.07	0.04	
V_H	7.00		6.50	9.80	10.70	9.50	15.60	13.30	5.20	12.10	7.60	9.00	4.70	
UTR2P/UTR2I														
n	6	2	17	10	13	16	13	34	8	22	6	32	9	2
min	3.50	4.18	2.07	3.12	2.24	2.20	3.62	2.64	4.76	2.95	5.48	1.00	3.88	4.69
$\bar{x}$	5.16	4.43	6.87	6.36	9.05	6.05	6.22	7.19	8.15	8.25	11.89	8.90	10.69	7.70
max	7.70	4.68	26.40	10.59	22.57	12.67	10.36	37.33	13.45	22.33	20.00	51.00	46.25	10.70
Sx	0.69		1.46	0.89	1.83	0.91	0.61	1.10	1.02	1.06	2.44	1.62	4.46	
Sd	1.68		6.02	2.81	6.58	3.63	2.21	6.39	2.87	4.95	5.99	9.15	13.39	
V_H	33.9		88.9	45.3	74.1	60.9	36.2	89.5	36.3	60.7	52.5	103.6	128.7	
LTR2/LTR1														
n	6	2	17	9	13	15	14	33	11	22	8	33	10	2
min	1.03	1.09	0.87	0.83	0.68	1.00	0.65	0.83	1.02	0.61	1.05	0.86	1.01	1.08
$\bar{x}$	1.10	1.17	1.10	1.11	1.07	1.12	1.07	1.12	1.08	1.11	1.12	1.12	1.11	1.22
max	1.15	1.25	1.25	1.34	1.30	1.22	1.38	1.27	1.16	1.41	1.22	1.50	1.27	1.36
Sx	0.02		0.02	0.05	0.04	0.02	0.05	0.02	0.01	0.03	0.02	0.02	0.03	
Sd	0.05		0.08	0.14	0.14	0.06	0.20	0.09	0.05	0.15	0.06	0.11	0.09	
V_H	3.80		7.40	13.00	12.40	5.50	18.10	8.10	4.70	12.80	5.50	9.00	8.30	
IMP														
n	6	2	17	11	13	16	14	32	12	23	8	33	10	2
min	10	1	6	2	9	1	7	3	5	1	5	1	2	7
x	14.00	5.00	15.53	6.82	16.31	9.75	14.71	7.88	13.17	6.74	13.75	6.09	6.50	8.00
max	22	9	36	12	23	16	21	17	24	11	27	15	15	9
Sx	1.70		1.74	0.87	1.18	0.96	0.98	0.58	1.75	0.54	2.47	0.59	1.18	
Sd	4.16		7.19	2.89	4.27	3.83	3.67	3.26	6.05	2.61	6.98	3.39	3.75	
med	13	5	14	7	18	10	15/16	7	11/12	7	13	5	5/6	8
V_H	31.00		47.00	43.30	26.70	39.90	25.40	41.70	46.90	39.10	52.40	56.10	58.70	
MP														
n	6	2	17	11	13	16	14	32	12	23	8	33	10	2
min	59	43	55	51	64	57	53	57	66	60	65	67	80	61
x	66.83	54.00	74.06	69.00	79.85	71.19	80.43	71.94	79.17	76.26	80.75	91.97	93.20	75.50
max	75	65	99	84	92	87	100	95	89	99	102	114	118	90
Sx	2.30		2.60	2.61	2.39	1.72	3.24	1.34	2.29	2.26	4.37	2.15	4.24	
Sd	5.64		10.72	8.64	8.62	6.86	12.13	8.10	7.95	10.82	12.37	12.36	13.64	
med	66/67	54	74	69	84	72/73	79/80	72	81	75	79/80	92	88	75/76
V_H	8.80		14.70	12.80	11.00	9.80	15.40	11.40	10.30	14.30	15.80	13.50	15.10	

Fig. 6. SEM micrograph of left corner of the oral disk of a *graeca* tadpole (stage 38) from Krathis potamos, Greece (NMW 29181)

Through all size classes up to TL ≤ 55 mm, mean numbers of MP increase constantly from 54 to 93 in Greek, and from 67 to 81 in Italian larvae. There are always significant differences ($\alpha \leq 0.1$) between Italian and Greek specimens. However, in size classes TL < 45 mm, Italian larvae have more papillae than Greek ones, while in longer larvae the contrary is observed (Table III).

Inframarginal papillae (IMP) are frequently found in the corners of the mouth or solitary inside the marginal papillae. Their number is significantly ($\alpha \leq 0.01$) higher in Italian than in Greek tadpoles of TL ≥ 30 mm (Table III).

In tadpoles at stages 27 through 41, there are usually 4-5 rows of keratodonts (*tooth rows*) in the anterior and 4 in the posterior lip. Keratodonts are disposed in single series on each ridge. In all tooth rows of tadpoles at stages 36-38, density of keratodonts is 7-8 per 100 µm; they are 70-80 µm long and their apical portions are spatulate with 12-14 acute marginal denticles each (fig. 7).

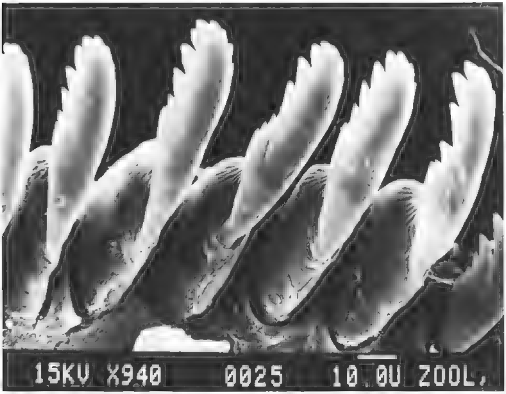

Fig. 7 SEM micrograph of keratodonts of a *graeca* tadpole (stage 38) from Krathis potamos, Greece (NMW 29181)

The outermost upper row (UTR1) and the outer three lower rows (LTR1-3) are continuous and almost equal in length. The innermost lower row (LTR4) reveals a short median gap without exception in our specimens; however, according to BOULENGER (1891a-b), it may also be continuous. Width of median gap is wide in UTR3-5, and moderate to short in UTR2 (Table III). Ratios LTR2/LTR1 and UTR2P/UTR2I in Italian and Greek larvae do not differ significantly.

Both lateral extension of upper tooth rows and length of their left and right portion decrease in centripetal direction; the portions of the innermost extremely short row (UTR5) bear a few keratodonts only, and may be unilateral or even absent. Absence is more frequent in, but not restricted to, early developmental stages.

In both Italian and Greek tadpoles, the total number of tooth rows slightly increases during development. Two tooth row formulae were found frequently: 4/4 (in 30 specimens of *italica* and 29 of *graeca*) and 5/4 (in 53 and 164 specimens, respectively). Two much rarer formulae were observed exclusively in *graeca*: one specimen (stage 39) unilaterally showed a distinct innermost UTR6 (formula 6/4); in five specimens (stages 29, 33, 39, 40,

Fig 8 — Buccal floor of a *graeca* tadpole (stage 38) from Nea Figalia, Greece (NMW 27637).

41), a short outermost, fifth LTR, one fourth to one tenth of the length of LTR1, was present in a median position (formula 5/5).

The *jaw sheaths* (beak) are robust with dark pigmentation, the upper cutting edge is gently "M"-shaped, the lower one "U"-shaped; there are about 5 serrations (45-50 µm high) per 100 µm in both sheaths of tadpoles of stages 36-38.

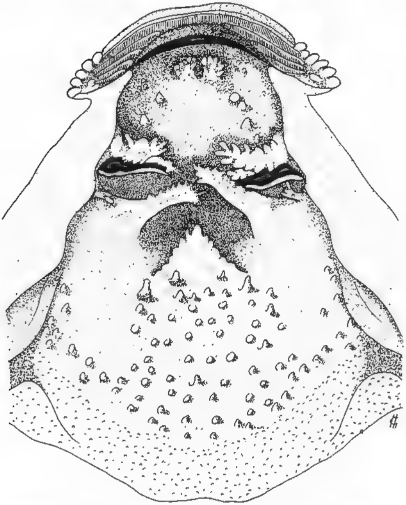

FIG. 9. - Buccal roof of a *graeca* tadpole (stage 38) from Nea Figalia, Greece (NMW 27637).

BUCCOPHARYNGEAL CAVITY

In the *buccal floor* (fig. 8), two pairs of stout, jointed ventral infrarostral pustulations form a semicircular arch within the median third of the prelingual area The pair of prelingual palps is large, with three slender, elongate, finely-limbed, and secondarily papillate lobes, long enough to reach out of the mouth.

Two slim cylindric lingual papillae rise in the posterior half of the distinct tongue anlage.

The buccal floor arena is scattered regularly with about 100 conical, elongate papillae, which are almost as long as the lingual papillae; there are few small pustulations in between. Prepocket papillae can be even larger and furcated or palp-like.

The margin of the velar apparatus describes a smooth, broad arch with three pairs of conical marginal projections corresponding to the filter cavities; the median portion of the velum is smooth-edged showing two further papilla-like projections on each side of the quite undistinct median notch. The glandular zone is broad, not markedly thickened, with distinct secretory pits, glottis and laryngeal disk are not exposed.

In the *buccal roof* (fig. 9), the prenarial area shows three pairs of tuberous papillae, arranged in a semicircular arch; the most anterior pair is polydactylous. The main axis of the internal nares is almost in a right angle to the main body axis. In the centre of the anterior narial walls a slender, papillate flap is rising on each side; medially, the wall is lined with a few minor pustulations. The posterior walls of the nares are smooth-edged valves with a slight lobe towards the midline on each side. There is a single pair of slender, elongate postnarial papillae, with a line of pustulations on the anterior margin, and only one pair of small, cylindric lateral ridge papillae with two or three terminal pustulations which may be accompanied by two tiny pustules each. The median ridge is forming an almost isogonic triangular flap; its lateral margins are bordered by three or four pustulations.

The high number of about 70 buccal roof arena papillae corresponds to that in the buccal floor, but the dorsal ones are markedly shorter. The dorsal velum is well developed, showing a broad zone with distinct secretory pits.

No obvious differences were found between Italian and Greek tadpoles.

Discussion and conclusions

Morphological adaptations to life in flowing waters

Most of the tadpoles of *graeca* and *italica* on which this study is based were collected in flowing waters. small brooks, torrents of various sizes or larger rivers (Table I). Only one series of *italica* was collected in part in a river (Fiume Savuto) and in part in a pond in the bed of this river and close to the flowing river itself: probably the eggs were laid there before the pond was isolated from the river by the lowering of its level.

The larvae of *graeca* and *italica* are highly adapted to flowing waters by both external and buccopharyngeal characters. These comprise the slightly depressed body, the relatively long tail with low dorsal and ventral caudal fin, the former barely reaching the trunk, as well as the subterminal oral disk with the highest number of tooth rows among European ranine larvae.

In the lateral corners of the oral disk, besides the solitary inframarginal papillae, two papillate ridges are descending towards the basis of the beak on each side (figs. 5-6). In this region, folds and additional papillae are often seen in anuran larvae, but distinct pairs of ridges have not been reported before; they might support the suctorial function of the oral disk in separating upper and lower "lips", and thus, possibly enable maintainance of low-pressure in the posterior portion while the anterior part may be loose. Though the importance of oral disk suction in flowing waters is evident, too little is known on mechanics of the peribuccal structures in feeding and adhesion for clear functional interpretation.

The pair of prelingual palps, long enough to reach out of the mouth, is a feature of the stream-adapted, bottom-feeding type as characterized by WASSERSUG (1980).

The number of buccal floor papillae (about 100) is at least twice that of *R. temporaria* given by VIERTEL (1982). In European ranine frogs, usually 40 to 60 papillae are found in this area, the lateral ones tending to be more elongate, the median ones often being low pustules. In general, these papillae are more numerous and elongate in stream-adapted larvae feeding on a self-generated suspension, and are serving as a coarse pre-filter (WASSERSUG, 1980). This also has been noted by GRADWELL (1972) for tadpoles of *Rana fuscigula* which live in "quiet pools in cool mountain streams".

The larvae of *graeca* and *italica* belong to the few lotic European tadpoles which also include the larva of the Majorcan midwife toad, *Alytes muletensis* (VIERTEL, 1984), the tadpoles of *R. iberica* and *R. pyrenaica* (SERRA-COBO, 1993), and possibly at least of some populations currently referred to *R. temporaria* and to the *R. macrocnemis* complex.

As concerns the ecomorphological guilds of exotrophic anuran larvae (ALTIG & JOHNSTON, 1989), *graeca* and *italica* have to be assigned to the lotic, rheophilous type, moderately expressing the characters of the "clasping" subtype

COMPARISON WITH OTHER EUROPEAN FROGS OF THE GENUS *RANA*

In four European brown frog species there is a tendency towards irregular development of the outermost lower tooth row and the innermost upper tooth row, concerning UTR5 in *graeca* and *italica* (present paper), UTR4 in *R. t. temporaria*, and UTR3 in *R. dalmatina* and *R. arvalis wolterstorffi* (GRILLITSCH & GRILLITSCH, 1989). Although early posthatching stages are not on hand, *graeca* and *italica* seem to fit into the general pattern of tooth rows development within the European brown frogs, which means: rows of keratodonts being additional to the basic formula of 2/3 show retarded ontogenetic appearance, are added centripetally in the upper, centrifugally in the lower lip, and reveal the more susceptibility to alterations the later they occur (GRILLITSCH & GRILLITSCH, 1989). Both retarded ontogenetic appearance and irregular formation suggest these additional tooth rows to be of young phylogenetic age

For differential diagnosis to sympatric *R temporaria*, *R. dalmatina* and green frogs larvae, the tooth rows formulae of *graeca* and *italica* (4-5/4 in *italica*, 4-6/4-5 in *graeca*) appear to be the most suited and easy to handle external character It may fail in very young specimens (TL < 20.0 mm) and in advanced specimens with already reduced number of tooth rows, and then may lead to confusion, especially with *R. temporaria*.

In the samples studied, the following three buccopharyngeal characters of *graeca* and *italica* (stages 36-38) showed distinct differences compared to the other European brown frog tadpoles for which these characters were already described:

– In ranine frogs, two or four lingual papillae occur, the latter type being most common (HAMMERMAN, 1964; VIERTEL, 1982; INGER, 1985). According to VIERTEL (1982), the number of lingual papillae is useful to separate European brown frogs (subgenus *Rana (Rana)* sensu DUBOIS, 1992) from European green frogs (subgenus *Rana (Pelophylax)* sensu DUBOIS, 1992), the former developing four, the latter two lingual papillae. Yet, *graeca* and *italica* tadpoles have two papillae, which contradicts the above classification.

– Comparing the total counts of velar marginal projections, VIERTEL (1982) gives them as 5-6 in European brown frogs and about 10 in European green frogs; *graeca* and *italica* with a number of 10 match the latter. This cancels the character for group clustering but separates *graeca* and *italica* from the other brown frogs.

– In *graeca* and *italica*, the longitudinal axis of the internal nares is almost in a right angle to the main body axis; this is different from all other European *Rana* species where the choanae form an anteriorly opened, obtusely angled "V" (VIERTEL, 1982).

All the characters mentioned above support the proposal of DUBOIS (1992) to recognize, within the subgenus *Rana (Rana)* s. str., a distinct species group (*Rana graeca* group) for *graeca* and *italica*.

THE STATUS OF *GRAECA* AND *ITALICA*

Larvae from Italy and Greece could not be distinguished unequivocally from each other on the basis of their buccopharyngeal morphology. However, *graeca* has a significant tendency to have more tooth rows in the anterior lip than *italica*, especially in older stages. Besides, there are slight but significant differences between them in a variety of external morphometric features (SV(TL)/stage; ratios VT/HT, UF/LF, VT/SV, SV/SU, RN/NP, PP/OD, NN/OD; numbers of MP and IMP). Depending on developmental stage these differences are of variable diagnostic significance. "Coefficients of difference" (GÉRY, 1962; MAYR, 1975) were calculated for every metric character in all size classes. Out of 70 coefficients, 66 (i.e. 94 %) were low (between 0.0 and 0.71), indicating that thereby less than 70 % of the individuals can be assigned correctly to one of the groups, Italy or Greece. Only four coefficients (Table IV) came close to or even surpassed the usual conventional degree (1.28) of subspecific divergence, suggesting that, with their help, 85-92 % of the individuals can be assigned to the right group. The more the tadpoles develop, the more evident become the differences between Italian and Greek larvae. The mean coefficient of difference of all 14 proportions increases from 0.22 (TL 25 0-29.99 mm) to 0.49 (TL 45.0-49.99 mm).

Discriminant analyses executed for 6 size classes revealed two isolated clusters (Italy and Greece), to which 87-100 % of the individuals were assigned properly (fig. 10).

This study therefore demonstrates the existence of a significant morphological dissimilarity between the tadpoles of Italy and Greece. Addition of this third piece of

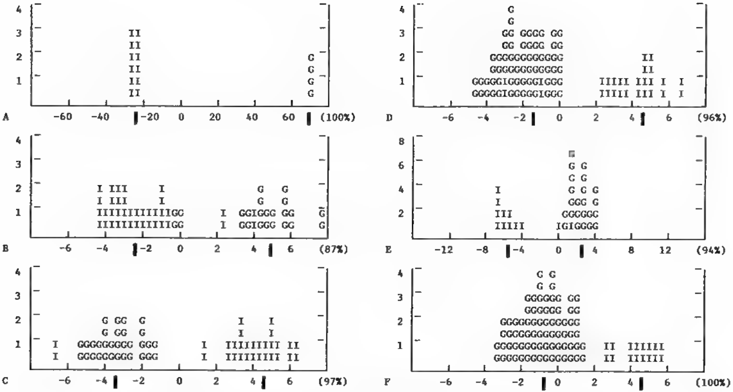

Fig. 10 — Six size classes (A: 20.0-24.99 mm, B. 25.0-29.99 mm; C: 30.0-34.99 mm; D: 35.0-39.99 mm, E: 40.0-44.99 mm, F. 45.0-49.99 mm) of 212 *graeca* (G) and *italica* (I) tadpoles clustered by discriminant analysis with stepwise variable selection. The percentage of proper assignement is indicated at the right end of the abscissa. Vertical bars (I) at the bottom symbolize class centroids. The ordinate represents the frequency (number of individuals), the abscissa shows canonical discriminant function scores.

Table IV. Ratios and size classes where coefficients of difference between *graeca* and *italica* are close to the usual conventional level of subspecific separation (1.28). For abbreviations see Table II.

Ratio	Size class	Coefficient of difference
VT/HT	40.00-44.99 mm	1.40
VT/HT	45.00-49.99 mm	1.03
PP/OD	45.00-49.99 mm	1 28
NN/OD	45.00-49.99 mm	1.08

evidence to the first two already available (adult morphology: Dubois, 1987; allozymes: Picariello et al., 1990; Capula, 1991; Gollmann, 1992), confirms that both forms should be treated as different taxons Should they be considered subspecies or species? Since these forms are fully allopatric, not connected by a contact zone, this question is difficult to answer (see e.g. the detailed discussion in Dubois, 1977), and at this stage of research we prefer to keep this question open. We disagree with several current authors regarding the taxonomic weight and meaning of "molecular distances" (see Dubois, 1988b: 50, for a criticism of the use of the name "genetic distance" for such indices): these distances can be based on the results of electrophoreses (e.g. Nei's or Rogers' distances), on immunological comparisons, or on nucleic acids hybridizations or direct comparison of their sequences. Contrary to what is believed by some current workers, including batrachologists (Cei, 1971; Crespo, 1972; Lanza et al., 1975, 1976, 1982, 1984; Busack et al., 1985; Capula et al., 1985; Busack, 1986; etc.), a high "molecular distance" between two allopatric populations or groups of populations is not *by itself* sufficient evidence that they belong to distinct species: it can just be one piece of evidence among others, with no more weight than evidence from morphology, mating call, chromosomes, etc. As analysed in detail by Pasteur & Pasteur (1980) and Pasteur (1985), there exists no such thing as a "specific level" of molecular differentiation· for example, two different good species may be separated by a "molecular distance" much weaker than that between populations of another species. Therefore, proper resolution of the status of *graeca* and *italica* will require additional work, dealing with other characters (e. g. hybridization, eco-ethology, mating calls, nucleic acids, chromosomes, etc.).

Résumé

La morphologie externe et l'anatomie buccopharyngée des têtards de *Rana [graeca] graeca* et *Rana [graeca] italica* sont décrites en détail. Ces caractères traduisent une bonne adaptation de ces têtards à la vie en eau courante. Les particularités buccales les plus notables sont le nombre élevé de rangées de kératodontes, le nombre élevé de papilles sur le plancher et le plafond buccal, et les grands palpes prélinguaux à lobes allongés.

Les têtards provenant d'Italie ressemblent beaucoup à ceux de Grèce. Toutefois, les deux groupes s'avèrent différer légèrement mais de manière significative l'un de l'autre pour un certain nombre de caractères. Ces résultats confirment l'existence de deux taxons distincts, sous-espèces ou espèces, *graeca* pour les populations des Balkans et *italica* pour celles des Apennins.

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